



Influence of nutrients, disturbances and site conditions on carbon stocks along a boreal forest transect in central Canada

J. S. Bhatti^{1,3}, M. J. Apps¹ & H. Jiang²

¹Canadian Forest Service, Northern Forestry Centre, 5320, 122nd Street, Edmonton, Alberta, Canada T6H

3S5 ²Department of Renewable Resources, University of Alberta, Edmonton, Alberta, Canada T6G 2H1

³Corresponding author*

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Abstract

The interacting influence of disturbances and nutrient dynamics on aboveground biomass, forest floor, and mineral soil C stocks was assessed as part of the Boreal Forest Transect Case Study in central Canada. This transect covers a range of forested biomes—from transitional grasslands (aspen parkland) in the south, through boreal forests, and into the forested subarctic woodland in the north. The dominant forest vegetation species are aspen, jack pine and spruce. Disturbances influence biomass C stocks in boreal forests by determining its age-class structure, altering nutrient dynamics, and changing the total nutrient reserves of the stand. Nitrogen is generally the limiting nutrient in these systems, and N availability determines biomass C stocks by affecting the forest dynamics (growth rates and site carrying capacity) throughout the life cycle of a forest stand. At a given site, total and available soil N are determined both by biotic factors (such as vegetation type and associated detritus pools) and abiotic factors (such as N deposition, soil texture, and drainage). Increasing clay content, lower temperatures and reduced aeration are expected to lead to reduced N mineralization and, ultimately, lower N availability and reduced forest productivity. Forest floor and mineral soil C stocks vary with changing balances between complex sets of organic carbon inputs and outputs. The changes in forest floor and mineral soil C pools at a given site, however, are strongly related to the historical changes in biomass at that site. Changes in N availability alter the processes regulating both inputs and outputs of carbon to soil stocks. N availability in turn is shaped by past disturbance history, litter fall rate, site characteristics and climatic factors. Thus, understanding the life-cycle dynamics of C and N as determined by age-class structure (disturbances) is essential for quantifying past changes in forest level C stocks and for projecting their future change.

Introduction

Boreal forests play an important role in the global carbon (C) budget (Apps et al., 1993; Dixon et al., 1994). The total C pool in forest ecosystems has been estimated to be about 1150Gt (Dixon et al., 1994) of which 49% is in boreal forests. In the boreal zone, 62% of the C is stored in dead organic matter (soils, detritus and other debris), 30% in aboveground biomass, and about 8% as below ground biomass (Apps et al., 1993) while

up to 95% of the N is stored in forest floor and mineral soil (Morris and Miller, 1994). Very high amounts of C and N in soil are due to short growing seasons and cool temperatures, both of which restrict production, decomposition rates and nutrient cycling.

Forest ecosystem C content is the result of interaction between climate, soil moisture, soil temperature, plant species, nutrient availability, soil texture, and disturbance regimes. These factors control the processes of primary production and decomposition which in turn affect C dynamics (Bonan and Van Cleve, 1992; Peng et al., 1998). Delineating the interacting processes, and the quantitative relationships

* FAX No: 780-435-7359

E-mail: Jbhatti@NRCAN.GC.CA

between them are keys to improved projections of C budget responses to climate change and to potential management intervention.

Changes in forest ecosystem C pools are driven primarily by the dynamics of the living biomass which are in turn strongly influenced by disturbance regimes (Larsen and MacDonald, 1998). Large, uncontrolled forest fires of natural origin are a major disturbance agent across the western boreal forest of Canada (Weber and Stocks, 1998). Repeated disturbances, such as fires, result in landscape patterns with stands of different ages whose distribution reflects the contagious nature of the disturbance (Li and Apps, 1996). Disturbances also alter the forest productivity, may release C directly into the atmosphere (fires) and transfer large amounts of C from biomass into detritus, soils or forest products. Small changes in weather patterns over periods of years to decades and longer can change the disturbance frequency, which can produce significant shifts in the age-class distribution and spatial arrangement of the forest (Gardner et al., 1996). With increasing disturbance frequency, a greater proportion of the forest is found in younger age classes. Young and immature stands in the landscape contain less C than mature stands, but have higher net ecosystem production, other factors being the same. Therefore information on age-class structure is essential for an accurate estimate of C content at a regional scale (Apps and Kurz, 1993).

Some forms of disturbance, such as outbreaks of defoliating insects, may do considerable damage, but not lead to significant and spatially correlated mortality (i.e., are not stand replacing). With such disturbances, there are no changes in the age-class distribution but accumulation and distribution of biomass C are changed. Shifts in climatic conditions such as repeated drought or warming trends may alter forest stand susceptibility to insect infestation. Consequently, even in the absence of large scale mortality, changes in the disturbance regime induced by alteration of climatic conditions results in C losses (or gains) from the forest ecosystem if other conditions are unchanged (Apps and Price, 1996; Kurz et al., 1998).

Nitrogen is a key determinant of C stocks and sequestration in boreal forest ecosystems (Kimmins, 1996; Shugart et al., 1992). The availability of N plays a central role in determining the leaf area index, carbon allocation, internal nutrient cycling, litterfall, soil decomposition, and vegetation species in some forests (Boring et al., 1988). The C storage capacity of forest

stands at high latitudes is strongly linked to their ability (1) to sequester N and other nutrients from external sources, (2) to absorb and transfer N from the soil (with low C: N ratio) to vegetation (higher C: N ratio), (3) to increase the C: N ratio of ecosystem components, or (4) to exploit a combination of these factors (Townsend and Rastetter, 1996).

Changes in other environmental factors such as moisture and temperature regime might also alter any of the processes relating to N constraints (Kimmins, 1996). In boreal forests, inputs of N at a given site are primarily through atmospheric deposition and N fixation. Inputs through translocation and runoff are minor in central Canadian boreal forests since the topographical relief is negligible (Price and Apps, 1995). Disturbance results in depletion or enrichment of N from a site. For example, N losses from a site occur after disturbance through the removal of harvested biomass (Bhatti et al., 1998; Foster et al., 1997; Olsson et al., 1993), leaching (Cole, 1995; Harrison et al., 1995), gaseous emissions including fire combustion products (McLean and Wein, 1977; McMurtrie and Dewar, 1997; Raison et al., 1985), or erosion (Harrison et al., 1995). Large disturbance impacts are likely to be found in Canadian boreal forest stands because of their low N reserves (Kimmins, 1996). Studies examining the effect of disturbance have shown large amount of N can be lost from forest stands (Morris and Miller, 1994; Raison et al., 1985). Such losses, however, may be partially offset by enhanced N fixation (Cole, 1995) and the increased mineralization associated with higher decomposition rates after disturbance (Entry and Emmingham, 1995; Qualls et al., 1991). To sustain the ability to sequester C, the N losses after disturbance must be balanced by N inputs through atmospheric deposition, biological fixation, or application of nitrogenous fertilizers.

Recently available data are used in this paper to assess i) the relationship between N and C stocks in aboveground biomass, forest floor, and mineral soil, and ii) factors affecting the N dynamics along the Boreal Forest Transect Case Study (BFTCS) in central Canada. BFTCS sites are particularly useful for examining the role of nutrients in C sequestration not only because these boreal ecosystems are consistently N limited but also because this region has been well studied as part of the Boreal Ecosystem-Atmospheric Study (BOREAS) (Halliwell and Apps, 1997a-c; Peng and Apps, 1998; Peng et al., 1998; Price et al., 1999a, b; Sellers et al., 1998).



Figure 1. Location of the Boreal Forest Transect Case Study (BFTCS) in Canada showing major ecological zonations and the BOREAS study area.

BFTCS study area

The BFTCS is an extensive, long-term study based on a contiguous, mid-continental transect that crosses an important climate-sensitive northern terrestrial biome (Fig. 1). The BFTCS is identified as one of a number of key ecosystem transect studies of the Global Change and Terrestrial Ecosystems (GCTE) core project of the International Geosphere-Biosphere program (IGBP) (Koch et al., 1995). The studies along BFTCS provide information about the current structure and function of Canadian boreal forests and their response to changing climate (Price and Apps, 1995; Sellers et al., 1997). The nominal transect covers approximately 1000×100 km with generally flat topography and is oriented southwest-northeast (Fig. 1). This orientation is along an ecoclimatic gradient, with vegetation ranging from agricultural grasslands in southern Saskatchewan through the boreal forest in the central portion to the tundra in northern Manitoba (Ecoregions Working Group, 1989; Price and Apps, 1995).

Climatic fluctuations account for much of the variation in vegetation and productivity differences along the BFTCS (Peng et al., 1998). Both temperature and precipitation play important roles in the growth and survival of boreal species along the transect (Price et al., 1999a). In the northeast end of BFTCS, low temperatures (but higher precipitation) dominate, while in the southwest low moisture content (but warmer growing conditions) plays the dominant role (Hogg, 1999; Peng et al., 1998; Price and Apps, 1995; Price et al., 1999b). Precipitation decreases (AES, 1983) together with a steady increase in annual potential evapotranspiration (PET) from the northeast to southwest (Fig. 2). This gradient is a major factor determining the current boreal forest distribution: growing season soil moisture deficits play a critical role in determining forest structure and productivity (Price and Apps, 1995; Price et al., 1999a,b; Sellers et al., 1997). Actual evapotranspiration is lowest at the two ends of the transect. In both the aspen parklands (south) and the subarctic woodlands (north), forest stands are sparse with open canopy, woodland structure (Apps and Kurz,

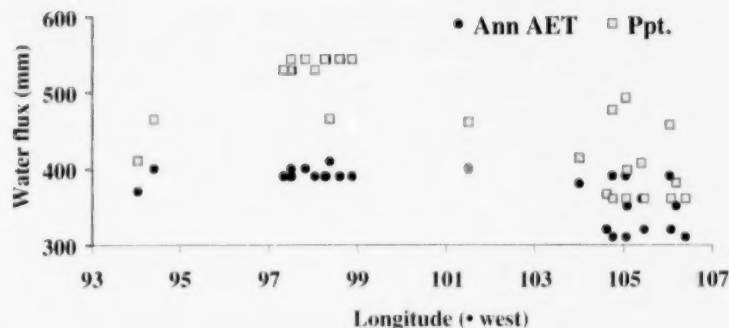


Figure 2. Annual precipitation and actual evapotranspiration along the BFTCS (data for period 1951–1980, data from AES, 1983).

1993) but the responsible mechanisms are different (BOREAS Science Steering Committee, 1991). Zoltai et al. (1992) reported that climate related stresses in the northern and southern part of the transect were responsible for the lower forest productivity found at both ends of the BFTCS.

Soil nutrient reserves also show systematic trends across the transect. Soil types vary from predominantly chernozemic in the southwest through a mixture of luvisols, humic–ferrie podzols and fibrosols (peat), overlying Canadian Shield bedrock in the north-eastern end (Agriculture Canada Expert Committee on Soil Survey, 1987). These systematic trends in soil type create a gradient of decreasing fertility from southwest to northeast (Price and Apps, 1995). The combined effects of climate and nutrient gradients as discussed above are postulated to be responsible for the maximum in aboveground biomass observed toward the middle of the transect area (Halliwell et al., 1995).

Data from 92 sites at 84 distinct geographical locations were used to estimate the aboveground biomass along the BFTCS (Halliwell and Apps, 1997a,b). The dominant plant species on these sites included *Populus tremuloides* (aspen), *Picea mariana* (black spruce), *Pinus banksiana* (jack pine), and *Picea glauca* (white spruce). At each site, standard measurements of stand density, basal area and standing volume were combined with data on species allometry to estimate vegetation biomass (Halliwell and Apps, 1997b). Soil samples were collected from co-located soil plots at each site and each horizon analyzed for bulk density, C, N, and other chemical properties (Halliwell and Apps, 1997c). Soil drainage was assessed qualitatively for all the sites. Only upland sites with a mineral soil horizon were included in the analysis reported here; organic soils (e.g., peat) are not included,

as the processes determining site productivity and C accumulation are quantitatively different in such soils.

Disturbances in Canadian boreal forests

The major stand-replacing agents of disturbance in Canada's boreal forest are fire, insects and harvesting (Kurz et al., 1995a). Natural disturbances have both endogenous and exogenous causes, and operate over a wide range of size, frequency, predictability, and timing (season of the year), as well as magnitude of impact (Attiwell, 1994). In the period 1970–1990, natural disturbances in Canada appear to have increased in frequency at a national scale (Kurz et al., 1995b). The annual area burned increased by nearly 300% in north American boreal forests, increasing from 1.2×10^6 ha in 1960 to 3.2×10^6 ha in the 1990s (Zimov et al., 1999). In some regions, the changes are greater than the average; in others less (Kurz and Apps, 1999).

Historically in central Canada, wild fire has been the major agent of disturbance followed by pests and diseases. Harvesting has accounted for less than 4% of the annual losses prior to 1995 in the region (Kurz and Apps, 1999). Between 1980 and 1994, about 20% of the BFTCS area was disturbed by stand-replacing fires (Weber and Stocks, 1998). The mean fire return interval for some regions in Alberta and Saskatchewan was reported to be as low as 34 years (Larsen and MacDonald, 1998).

In addition to their effects on the stand age-class (Van Wagner, 1978) and species composition, wild-fires can also have a significant impact on the site characteristics. For example, there is evidence that the near-ground air temperature of recently burned areas is elevated (Päätaalo, 1998). This effect may in turn

lengthen the growing season for the disturbed site for several years, release nutrients (making them available for plant uptake) and decrease soil acidity and depth of the organic layer. A low or moderate intensity fire may thus mobilize nutrients and accelerate the regrowth of the forest stand. In contrast, an intense fire may deplete the soil of volatile nutrients (N, S, and P) (Raison et al., 1985) and result in longer term decreases in productivity and C sequestration of that site (Johnson, 1992).

Biomass C stocks and their dynamics

C pools in aboveground biomass

Aboveground biomass along the BFTCS varies between 2.2 and 15.4 kg m⁻² (average 7.6 kg m⁻²) for well drained sites and 4.0 to 18.7 kg m⁻² (average 8.6 kg m⁻²) for poorly drained sites (Bhatti and Apps, 2000). The higher biomass under poorly drained conditions is associated with the presence of many mature black spruce stands (Halliwell et al., 1997a); such sites are less susceptible to fire disturbance. High and low productivity stands are found in both drainage categories. The biomass values reported by Bhatti and Apps (2000) are within the range of inventory values for the prairie provinces (Bonnor, 1985); boreal forests in Alberta have an average of 7 kg m⁻², Saskatchewan 7 kg m⁻², and Manitoba 3 kg m⁻². Conversion of biomass to C indicates that C storage in these boreal forests range from 1.1 to 7.7 kg C m⁻² for well-drained sites and 2.0 to 9.3 kg C m⁻² for poorly drained sites. These estimates are consistent with values of 0.5 to 5.4 kg C m⁻² (average 2.4 kg C m⁻²) reported by Simpson et al. (1993) from direct measurements for western Canada's boreal forest. The biomass C values reported by Bhatti and Apps (2000), however, are lower than the 5–15 kg C m⁻² reported for the Lake States forest (Grigal and Ohmann, 1992). The difference may reflect real ecological variation between the ecoclimatic zones (Ecoregions Working Group, 1989).

Influence of disturbance on biomass C pools

The amount of C stored in biomass at a specific site depends on the seral phase and stage of stand development and, hence, on the site-specific disturbance history. During periods of decreasing disturbances, the age distribution shifts to the right so that more stands reach their mature and over mature growth phase — for boreal forests these are relatively even-aged stands

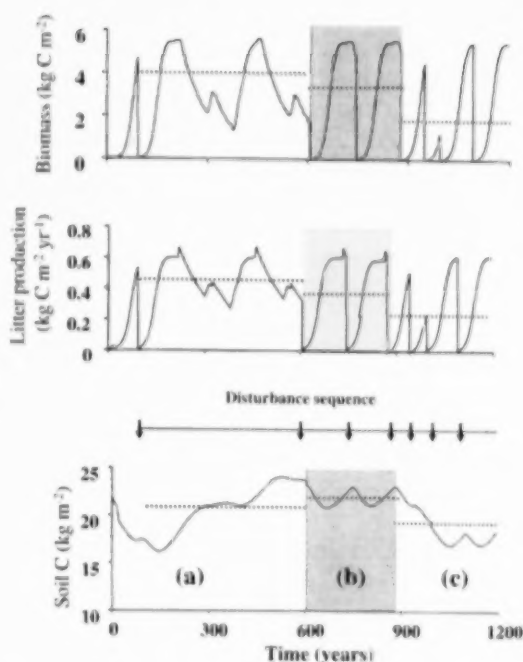


Figure 3. Simulated biomass, litter fall and soil C pools using a 1200-year segment of a random disturbance sequence (average 100-year return period over 7000 years) in a boreal forest stand. The dotted line represents the average value in each interval. Intervals A, B, and C indicate portions of the sequence that have periods of apparent low, medium and high disturbance respectively (modified from Bhatti et al., 2000a).

aged 100–200 years and older (Kurz and Apps, 1999). The biomass C content of these older forests is at, or near the potential maximum, but the rate of C sequestration is relatively low (Houghton et al., 1999). Changes in the disturbance regimes can thus have a significant influence on both the C stocks and their source-sink function.

To examine the variation of C stocks with changes in the disturbance regime, Apps et al. (2000) performed a simulation experiment with a 7000-year random disturbance sequence having an average return interval of 100 years over the record. A 1200-year portion of this random sequence exhibited transitions between periods of low, medium and high disturbances (Fig. 3). Changes in the biomass and other C stocks during these transitions were analyzed with a simplified version of the Carbon Budget Model of the Canadian Forest Sector (CBM-CFS2) described by Kurz and Apps, 1999.

The experiment by Apps et al. (2000) showed that for a given site and forest type, the site history—

specifically, the time since last disturbance—is a primary determinant of the biomass C pool. For example, while the absolute C content depended upon the species and productivity, simulated stand biomass C pools during an apparent period of low disturbance were 20–22% higher than the average over the 1200-year period (Fig. 3). During periods of increasing disturbances, more stands are shifted to the regeneration and immature growth phases and fewer, for example, reach the age of peak productivity (ca. age 50). During periods of higher disturbance, biomass C accumulation rates were relatively high but C stocks were about 44% lower (Fig. 3) than the temporal average for the entire simulation period of 1200 years.

The decrease in stand biomass C stock with frequent disturbances may be further exacerbated by N constraints (Kimmins, 1996). Disturbances alter the total nutrient reserve and rate of nutrient release in the stand. Increases in disturbance frequency or intensity causes transient loss of N. The highest N depletion may be associated with direct biomass removal (especially of nitrogen rich components such as foliage) from the site. The rate at which N is re-released by the forest floor due to the large influx of litter with high C:N ratio immediately after the disturbance may also be reduced through immobilization in woody debris. Therefore, as the disturbances increase, there may be a long term decline in the carrying capacity—and ability of the forests to return to the original C level—in response to the loss of nutrient capital (Kimmins, 1996; Nambiar, 1996).

Decline in the net C accumulation in biomass of mature and over-mature stands has been attributed, in part, to a change in nutrient cycling with stand age (Binkley et al., 1995; Foster et al., 1995; Frazer et al., 1990; Gholz et al., 1985; Paré and Bergeron, 1995). Various authors have postulated that: (i) older forests become N deficient due to a slow down in N cycling due to N immobilization in the forest floor; (ii) there is a shift with age in N uptake from mineral soil to uptake from forest floor; and (iii) as stand biomass ages, more of its N requirement is met by internal retranslocation than by uptake from the soil, particularly on less fertile sites. The decrease in N mineralization rate in the forest floor of mature forest stands has also been attributed to the presence of several free organic acids known to suppress N mineralization (Frazer et al., 1990; Pohlman and McColl, 1988) and enhanced water logging conditions (Paré and Bergeron, 1995).

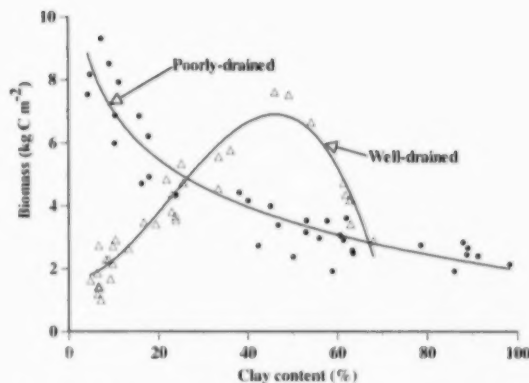


Figure 4. Relationship between percent clay content and above-ground biomass under well-drained and poorly drained conditions along the BFTCS (modified from Bhatti and Apps, 2000).

Influence of site properties on biomass C pools

The aboveground biomass depends on the soil clay content differently for well-drained and poorly drained conditions (Fig. 4). The relationship between soil clay content and aboveground biomass suggests that soil clay plays a major role both in providing nutrient storage sites and a physical environment for plant growth. Under well-drained conditions, aboveground biomass increases with clay content over an initial range, but then decreases rapidly above a clay-content threshold of about 45%. Limitation of biomass growth above this threshold may be due to restriction of soil rooting volume and poor aeration. Support for the latter hypothesis was given by Wang and Klinka (1996) who reported that fine textured soils can introduce anoxic conditions that adversely affects vegetation growth.

Under poorly drained conditions, there is an exponential decrease in aboveground biomass with increases in clay content (Fig. 4). Poor drainage adversely influences the available rooting volume, soil aeration, and soil temperature. Under poorly drained conditions, the less favorable conditions for root growth are directly expressed in aboveground productivity (Gale and Grigal, 1987). Lower aboveground biomass of spruce–fir forests in Maine (Williams et al., 1991) and willows (Labrecque et al., 1994), have been reported for poorly drained sites relative to well-drained sites. Under waterlogged conditions, Jeglum (1974) concluded that increases in clay content retards black spruce growth due to anoxic (or hypoxic) conditions and reduced N availability. Labrecque et al. (1994) also observed that the uptake of N on poorly drained sites was lower than in well-drained sites.

Influence N on biomass C pools

Boreal forests have a relatively tight N cycle (Kimmins, 1996). The N requirements of trees in boreal stands are met primarily by internal cycling rather than by N-fixation or from external sources such as N deposition (Foster et al., 1995). This reliance on internal N recycling arises because the rates at which N is supplied from external sources are generally low relative to N demand by the overstory vegetation and soil micro-organisms. Using data compiled by Ro et al. (1995), the average deposition rate in the period 1980 to 1994 is estimated to range from 1.8 to 2.5 kg N ha⁻² yr⁻¹ in Saskatchewan (south west end of transect), and from 2.1 to 2.2 kg N ha⁻² yr⁻¹ in Manitoba (north east end)—and has been relatively stable for at least the last two decades of the 20th century. These rates are within the range of N deposition reported by Shannon and Sisterson (1992). From these data, it is clear that deposition meets only a small portion of N requirement of boreal forest stands in the study region.

In long-term field trials in southern Ontario boreal forests, Foster et al. (1995) observed that mature jack pine stands obtained 50–60% of their N needs through uptake from the forest floor and soil while the remaining 40–50% was supplied by internal retranslocation. However, as the stands mature, there is a reduction in the rate of N uptake from the forest floor due to increased competition from understory species and a lower N-mineralization rate (Binkley et al., 1995; Foster et al., 1995). The net N-mineralization rate fluctuates between 15 and 25 kg N ha⁻² yr⁻¹ in Canadian boreal forests (Peng et al., 1998), an estimate that is consistent with the 15 to 51 kg N ha⁻² yr⁻¹ reported by Nadelhoffer et al. (1999) for North American boreal forests.

Site drainage has a strong influence on the N availability through its influence on N mineralization. Nitrogen mineralization is highly correlated with total N and soil texture (Pastor et al., 1984). Along the BFTCS, total N content increases with an increase in clay content (Fig. 5). However, increasing clay content creates poor drainage conditions which result in lower soil temperatures and reduced aeration—and therefore in reduced N mineralization (Kimmins, 1996). Ultimately, increased clay content leads to lower N availability (Klinka et al., 1994).

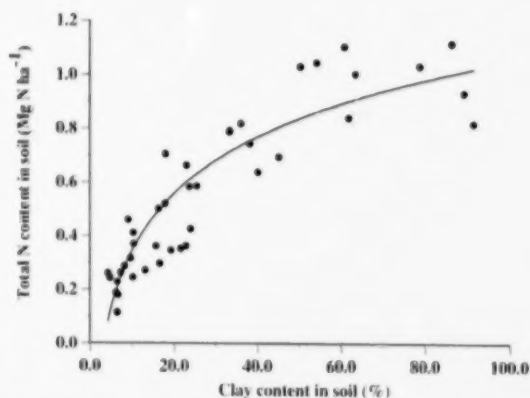


Figure 5. Relationship between soil clay content (%) and total N content along the BFTCS (modified from Bhatti and Apps, 2000).

Forest floor C stocks and its dynamics

C pools in forest floor

The average forest floor C stocks across the BFTCS reported by Bhatti and Apps (2000) was 3.7 kg C m⁻² with values ranging between 1.6 kg C ha⁻¹ and 5.0 kg C m⁻² depending on forest stand age and drainage conditions. The lowest C stocks were observed in well drained, recently burned sites and the highest stocks in very poorly drained, unburned sites (Rapalee et al., 1998). The C stocks reported by Bhatti and Apps (2000) along the BFTCS transect are close to the value of 3.3 kg C m⁻² reported by Vogt et al. (1986) for the global boreal forest, but much lower than that reported for southeast Alaska (8.3 kg C m⁻²) by Alexander et al. (1989). The estimate by Bhatti and Apps is higher than the 2.0 kg C m⁻² reported for the mountainous region of Oregon (Homann et al., 1995), or the 1.7 kg C m⁻² reported by Grigal and Ohmann (1992) for boreal-temperate transition zone forests in Minnesota, Wisconsin, and Michigan.

Forest floor C stocks can be empirically related to the N concentration in the forest floor along the BFTCS (Fig. 6). The N concentration explains 62% of the variation in observed forest floor C stocks. Hence, higher productivity on N rich sites is empirically correlated with higher forest floor C stocks and increasing N would be expected to be associated with increased forest C stocks (all other factors, including disturbance regime, being equal). Indeed, Van Cleve and Moore (1978) observed a significant increase (12–18%) in surface C content after N fertilization of boreal aspen stands in Alaska over a 7-year period.

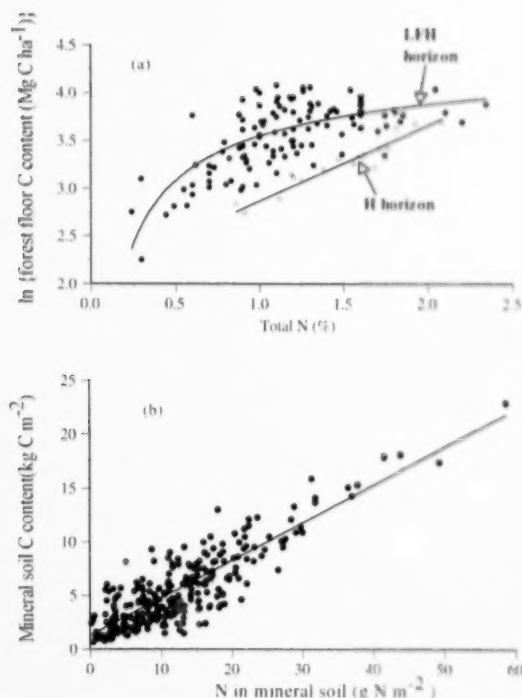


Figure 6. Relationship between C and total N in (a) the forest floor horizons and (b) mineral soil in boreal forests (modified from Bhatti and Apps, 1999).

Influence of disturbance on litterfall rate

The inputs of C to the forest floor are from litterfall and root detritus. Litterfall rates for boreal stands in central Canada were simulated with Carbon Budget Model of the Canadian Forest Sector (CBM-CFS2) (Kurz and Apps, 1999). CBM-CFS2 is a mass balance model that tracks C uptake by forest biomass and its subsequent transfer to detrital material, soils, forest products and to the atmosphere. The effects of disturbances on large scale C dynamics are explicitly represented in the model using historical records of annual disturbances (Kurz et al., 1995a). In CBM-CFS2, litter production associated with stand development (annual litter fall) and with disturbance debris is estimated separately for above-ground foliage, dead wood, bark, branches, as well as fine and coarse roots. Both these factors (litter production rates and size of litter components) influence the quantity and the quality (decomposability) of litter input to the detritus and soil pools. Simulated litter production for the boreal forest in central Canada was $0.35\text{--}0.38\text{ kg C m}^{-2}\text{ yr}^{-1}$ (Apps et al., 2000). These rates are consistent with the 0.27

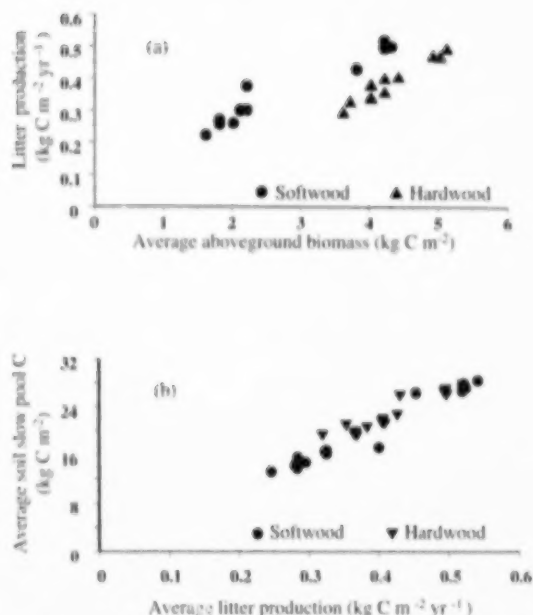


Figure 7. Relationship between average litter production and (a) total biomass C and (b) slow soil-pool C in boreal forest simulations (modified from Apps et al., 2000).

$\text{kg C m}^{-2}\text{ yr}^{-1}$ rates reported by Matthews (1997) for boreal forest, $0.12\text{--}0.33\text{ kg C m}^{-2}\text{ yr}^{-1}$ for aspen stands by Huang and Schoenau (1996), $0.46\text{ kg C m}^{-2}\text{ yr}^{-1}$ for jack pine, and $0.26\text{ kg C m}^{-2}\text{ yr}^{-1}$ for black spruce stands in Ontario observed by Morrison (1991). As expected, the simulated litter production rate is strongly dependent upon the biomass C (Fig. 7a).

Litter production rate is also regulated by the age-class structure and distribution, which are in turn related to the disturbance type and frequency (Apps et al., 2000). Litter production varies considerably among the stands making up the forest stands. The younger age classes have lower litter fall rates compared to those in the older age classes (Fig. 3). Consequently, mature stands have higher forest floor C stocks relative to younger age stands in boreal forests. Moreover, the physical size of individual litter components differs across the age distribution. The proportions of biomass C transferred to forest floor C stocks are also significantly influenced by the type of disturbance (Kurz et al., 1995a, b). Biomass C transfer to dead organic matter is expected to be greatest for insect-induced stand mortality, intermediate for fire (as some C will be released directly to the atmosphere as combustion products) and smallest for harvesting (where most of the woody material is transferred out

of the forest ecosystem to the forest product sector) (Apps et al., 2000).

Factors controlling decomposition

Several factors have been identified as controlling rates of decomposition in boreal forests, including temperature, precipitation, substrate quality and soil drainage (Trumbore and Harden, 1998; Van Cleve et al., 1991). On longer time scales (> 100 years), drainage conditions determine the decomposition rate. Compared to well-drained sites, poorly drained sites exhibit a lower decomposition rate along the BFTCS (Harden et al., 1998). Drainage conditions also modify the soil temperature which influences the decomposition rate. Under well drained conditions, the highest rates of decomposition along the BFTCS were observed (Trumbore and Harden, 1998) in sandy jack pine sites that experienced average July soil temperature of 13–16°C at 10 cm (Bubier et al., 1995). The coldest soils on the BFTCS (6–10°C at 10 cm), found in conjunction with permafrost or poorly drained conditions under mature black spruce stands, have the lowest decomposition rates (Trumbore and Harden, 1998).

The chemical quality and subsequent decomposability of surface detrital material are also modified by several abiotic factors, including site nutrient status, temperature and moisture content. Along the BFTCS, the average litter mass remaining at each site after 3 years range from 58 to 88%, increasing from northeast to southwest (Moore et al., 1999). In a long-term, large-scale litter bag study, Moore et al. (1999) found that three factors—mean annual temperature, mean annual precipitation and the ratio of Klason lignin (a resistant organic matter fraction) to N—explain 73% of the variance of percent initial mass undecomposed after three years. They also found that detritus from understory herbaceous species had higher decomposition rates than that of coniferous species. In addition, coniferous needles decompose much faster than roots and coarse woody debris (Hobbie, 1996).

These differences in decomposition rates can be explained by differences in initial nitrogen content in the plant tissues from which the detritus originates (Prescott, 1995), and hence on the N status of the site. The higher the lignin to nitrogen ratio in a given tissue, the lower is its initial rate of decomposition. Nitrogen concentrations in plant tissues are often positively correlated to the labile C content but negatively correlated with lignin (Taylor et al., 1991). Wessmann

et al. (1988) noted that an inverse relationship exists between the lignin concentrations of different canopy tissue and soil N availability in several forest ecosystems. In addition to limiting plant growth, lower site N availability thus results in lower N levels in plant tissues. But, as shown by Prescott (1995), low N with high tannin and lignin content in plant tissue make these tissues more resistant to decay. As a result, N-poor sites tend to have greater accumulation of the forest floor C stocks than N-rich sites (Vogt et al., 1995).

C stocks in the forest floor are strongly influenced by stand age. The influence of stand age on C stocks in the forest floor has been examined in boreal forest by determining C turnover rates. Forest floor C stocks increase with time after disturbance by fire (Harden et al., 1998). On jack pine sites, the forest floor turnover rates recover to near pre-disturbance levels within 20 years after fire (Weber, 1987). In contrast, lower rates of decomposition in younger stands of fire origin have been attributed to the presence of large amounts of slowly decomposing woody material (MacLean and Wein, 1978).

Soil C stocks and dynamics

On the BFTCS, mineral soil C shows more variability than does forest floor C. The average C content along the BFTCS in mineral soil was 11 kg C m⁻², with a range from 9 to 23.1 kg C m⁻² (Bhatti and Apps, 2000). The considerable range of soil C content was due to the variability in bulk density measurements along the BFTCS (Halliwell and Apps, 1997c). These C values are much lower than the 50 kg C m⁻² estimated by Tarnocai (1998) from interpreted soil carbon maps, but Tarnocai's estimates appear to also include organic soils (peat).

Bhatti and Apps' mineral soil estimates are comparable to those reported for global boreal forests by Post et al. (1982) (11.1–19.0 kg C m⁻²) and for North American boreal forests (13.5–19.5 kg C m⁻²) by Pastor and Post (1988). The soil C pool values along the BFTCS are also consistent with those reported for other regions. The average for 169 forest sites in Minnesota, Wisconsin, and Michigan was 10.5 kg C m⁻² (Grigal and Ohmann, 1992), while in north-central USA, the average for mineral soils was 10.7 kg C m⁻² (Franzmeier et al., 1985). The average for 149 forest profiles in the southeast Alaska was 18.5 kg C m⁻², with some profiles extending to a depth of 150

cm (Alexander et al., 1989). Differences in all soil forming factors, including climate, vegetation, parent material, topography, and moisture regime (Goulden et al., 1998) contribute to the differences between soil C pools of the boreal zone and adjacent transition-zone regions, but the trend to higher soil-C stocks in the colder and wetter regions is clear.

Soils become a long-term source or sink of C depending upon the type and history of disturbances (Bhatti et al., 2000b). Forest management also affects inputs to the soil particularly during harvesting (Scott et al., 1999). Above- and below-ground litter transfer has been identified as an important variable in controlling soil C stock accumulation. The simulated soil C content with CBM-CFS2 in the boreal forest of central Canada is directly related to the simulated litter production (Fig. 7b). As litter production increases, there is a steady increase in the soil C content. Litter production at a site also occurs stochastically with disturbances that provide large pulses of litter carbon (particularly coarse woody debris). The disturbance also changes the site microclimate and decomposition variables (Apps and Kurz, 1993; Scott et al., 1999) and hence the net balance of inputs and losses from the soil carbon pool.

The historical pattern of disturbances has a large effect on the soil C stocks at a given site. During a period of apparent low disturbance frequency, with higher forest biomass C contributing to higher litter production, the balance between decomposition losses and litter inputs is achieved at a higher soil carbon value (Fig. 3). Therefore, soil appears to act as a C sink during a transition to a lower disturbance frequency, as reported by Kurz and Apps (1996).

Conversely, during a transition to a period of more frequent disturbances, the soil C pool decreases and the soil appears to act as a source of C (Fig. 3). This phenomenon arises for three reasons. At the higher disturbance frequency, there is (i) a higher proportion of younger age stands which generate lower litter transfers (as described previously) (Scott et al., 1999), (ii) decreased input of coarse woody debris due to the decrease in proportions of older age stands (Harmon et al., 1990), and (iii) an increased rate of decomposition in detritus and in the soil C pool due to the changed microclimate (Bhatti et al., 2000b; Scott et al., 1999) and higher exposure associated with the younger stands. These situations might occur when forest biomass productivity is limited by climate conditions (for example), when input from disturbance is low because of severe fire loss or through harvesting,

or when the decomposition rate is high. Liski et al. (1998) observed similar results for the soils of boreal forests in western Finland. Under frequent fires, the amount of soil C could be 25% less than that estimated for a no-fire scenario. Johnson (1992) reported a significant soil C loss from high intensity wildfires and concluded that C loss increases with fire severity.

Soil C stocks are strongly related to soil texture. In general, soils with sandy texture have lower soil C relative to soils with higher clay content. Part of the reason for this is that detrital inputs are lower due to the lower productivity associated with lower nutrient reserves, as described above. Oades (1988), however, observed that the positive correlation between clay and soil C content may not represent a true cause-effect relationship because clay content is usually highly correlated with other factors, such as the presence of polyvalent cations, that also influence soil C accumulation. Polyvalent cations stabilize soil C compounds by a number of mechanisms, including electrostatic cation bridging of organic colloids and specific adsorption onto Fe and Al hydrous oxide surfaces (Oades, 1988; Torn et al., 1997). In addition to this polyvalent cation effect on soil C compound, physiochemical reactions between nitrogenous compounds and soil organic C is also important. Non-biological condensation reactions of phenols with ammonium contribute to the production of stable humus (Johnson, 1992). The edaphic environment also causes soil C compounds to become stabilized through binding with mineral colloids that protect them from microbial attack (Anderson, 1992; Torn et al., 1997).

Soil texture also determines the drainage condition; clay soils yield poor drainage conditions and reduce decomposition rates (Van Veen and Kuikman, 1990). On the BFTCS, the largest C stocks in mineral soils occur in poorly drained conditions (Rapalee et al., 1998; Tarnocai, 1998). Lower rates of decomposition are constrained by physical conditions (cold and wet) rather than by the ability of organic matter itself to decompose (Moore and Knowles, 1990). Even at low rates of decomposition, annual losses of C from poorly drained forested soils are significant and can largely determine the C balance of the forest stand (Goulden et al., 1998).

There are still uncertainties about the origin and dynamics of the large soil C pools in the boreal zone. Using radiocarbon data, Trumbore and Harden (1998) showed that in the northern BOREAS sites (Fig. 1), soil C stocks have been influenced more by the frequency and severity of wildfires than by the actual

decomposition rate of humic materials. Therefore, the dynamics of this large soil C may be dominated by the response of boreal forest vegetation to future changes in fire frequency and climatic conditions.

Conclusions

In boreal forest ecosystems, the potential for change in the net C balance is strongly influenced by the disturbance pattern and tightly constrained by N cycling. The BFTCS, oriented along an ecoclimatic gradient in central Canada, is well situated for studies directed at improving our understanding of these relationships that regulate C stocks and C exchanges with the atmosphere. In Canadian boreal forests, the disturbance frequency has increased over the period 1970–2000—a trend that appears to be consistent with that expected from climatic warming—and this has caused significant changes in the net carbon balance at the national scale (Kurz and Apps, 1999). Understanding how these changes might be exacerbated or mitigated in a changing global environment requires linking changes in stand structure with ecosystem processes in vegetation, litter and soils.

The amount of C stored and the rate of C accumulation in biomass, forest floor and soil both depend on the stage of stand development, associated nutrient cycling rates and site conditions. Disturbances are likely to cause considerable loss of nutrients from a site, altering the subsequent dynamics of the affected stand. Because nitrogen requirements in the boreal forest are met primarily by internal cycling, rather than from external sources, nitrogen removal by disturbances can have an adverse effect on soil N supply, and thus on the accumulation of C stocks over time.

The future C balance in boreal forest will largely depend on the type and frequency of disturbance and alterations to the N cycle under changing climate conditions. It will also depend on forest management practices that effect both the disturbance regime and the N cycle. Projected climate change scenarios for the boreal forest generally predict warmer and somewhat drier conditions, and are expected to change the disturbance pattern. Fire and insect predation regimes, for example, are historically sensitive to climate and are expected to change considerably under global warming (Volney, 1998; Weber and Flannigan, 1998). Altered boreal forest disturbance regimes—especially increases in frequency, size and severity—may release C from vegetation, forest floor, and soil at higher

rates than the rate of C accumulation in regrowing vegetation. The precise balance of uptake and release depends on the detailed processes, and especially interactions between the N and C cycles over the changing life cycles of forest stands. Quantifying the life-cycle dynamics of C and N at the stand level is essential for projecting future changes in forest level C stocks.

Will the net effect of such changes result in positive feedback to climate change and thereby accelerate global warming (Kurz et al., 1995b)? Scientific opinion remains divided on the answer: models that do not include disturbance effects or life-cycle dynamics tend to give negative feedbacks (increased C stocks) while those that attempt to include these effects tend to suggest transient positive feedback responses, with less growth or even losses in C stocks. The presence of large C stocks in a region that is likely to witness the greatest and fastest changes in climate in the greenhouse-gas enhanced world of the future (Houghton et al., 1995) gives cause for concern (Kirschbaum et al., 1995) and stimulates the search for the correct answer to this question.

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